

Metameric Segmentation and Homology.

By

Edwin S. Goodrich, F.R.S.,
Fellow of Merton College, Oxford.

With Plates 15 and 16.

In two recently published papers on the development of the fins of fish and on the segmentation of the head of Amphibia (12, 15), I had occasion to discuss incidentally the segmental relations of homologous organs, and to point out that, in the Vertebrates at all events, corresponding parts must be considered as fully homologous although occupying different segments of the body. In this paper I shall not attempt to define the nature of segmentation nor trace its origin, but shall merely try to show that a practical definition of the homology of an organ must not depend on its position in the series of segments. The subject of metameric segmentation has been very clearly dealt with by Sir E. Ray Lankester in articles on the Arthropoda and Metamerism in the tenth and eleventh editions of the 'Encyclopædia Britannica' (reprinted in vol. 47 of this journal). While giving a comprehensive review of the whole question of metamerism, he states thirteen "laws," or general propositions, with most of which what follows will be found in complete agreement. But, in spite of the results of Fürbringer (9, 10) from anatomical investigations, of Bateson (1) from observations on variation, and of others, there is, I think, a reluctance on the part of many anatomists to give up the idea that true homology depends on segmental correspondence. For instance, when discussing

the homology of the occipital condyle in the Amphibia and the Amniota, we are asked on what segments they occur, it being implied, if not expressly stated, that if they are not on the same segment they cannot be homologous.

The whole subject of homology and segmentation is very complex, imperfectly understood, and well worthy of further study. In the following paper I have endeavoured to put the theory clearly before the reader, and to come to some definite conclusion.

Let us consider first of all the paired limbs. No one will deny that the pectoral limbs are homologous throughout the land-vertebrates or Tetrapoda; and the same may be said of the pelvic limbs. By homologous we mean, in this case, that these organs can be traced back in an uninterrupted phyletic series to some common ancestral form. Yet the limbs do not necessarily occupy the same segments. For instance, in the Amphibia, while the pectoral limb belongs to segments 2, 3 and 4, in the Anura, it belongs to segments 2, 3, 4 and 5, in the Urodela; and while the pelvic limb occupies segments 8, 9 and 10, in the frog, it is in segments 16, 17 and 18 in Salamandra, in segments 20, 21 and 22 in *Necturus*, and still farther back in *Amphiuma*. Moreover, the sacral vertebra is the ninth in the frog, the sixteenth in Salamandra, and the twentieth in *Necturus* (see Diagram 1).

Among the living Reptilia the limbs vary considerably in position, especially the pelvic (Diagram 1). For instance, while in *Chamæleo* the brachial nerve-plexus extends over segments 3-6, and the pelvic plexus over segments 18-22, in *Lacerta* the former is from segment 6 to 9, and the latter from segment 26-31. In the limbless reptiles the nerve-plexus can still be found (Gadow (11a) Carson (5)). Thus *Amphisbæna* has a brachial plexus in segments 2, 3 and 4, and a pelvic plexus in segments 97, 98 and 99; *Bungarus*, a brachial plexus in segments 4 and 5, and a pelvic in segments 230 and 231; *Python* has a brachial plexus in the third and fourth segments, and a pelvic in segments 342-345. The sacral vertebrae are the twenty-fifth and twenty-sixth in

Stellio; the twenty-seventh and twenty-eighth in Ascalabotes; the twenty-ninth and thirtieth in *Lacerta*; the sixty-fifth and sixty-sixth in *Seps*. In birds also we find a remarkable inconstancy in the relative position of the limbs [for an admirable and detailed study of this question see Fürbringer's great monograph, (10)]. To take only three examples: in *Cypselus* the brachial plexus extends over segments 10-14, and the pelvic over segments 20-27; in *Podiceps* the brachial plexus occupies segments 15-18, and the pelvic segments 26-35; while *Struthio* has a brachial plexus in segments 17-21, and a pelvic plexus in segments 29-38. (see Diagram 1).

Even the Mammalia show considerable variation in the position of the pelvic limb, although that of the pectoral limb remains remarkably constant. The lumbo-sacral plexus of the rat includes the lumbar nerves 2-6, of the guinea-pig the lumbar nerves 3-6 and first sacral, of the gnu the lumbar nerves 4-6 and first and second sacral [Paterson (18)].

No less conspicuous is the shifting of the paired fins in fishes, as will be easily seen on consulting Diagrams 2 and 3.

In the foregoing account the genetic relation of the limbs to the segments has been determined by the nerve-supply in the adult. This is amply justified by a study of the development, which shows that any change of position during ontogeny, caused by the shifting of the limb-rudiment from its place of origin, is insignificant. The limb is not formed on one set of segments, and subsequently transferred to another region and supplied by new nerves. On the contrary, limbs arise in the embryo in that region which they occupy in the adult. As a rule several segments contribute to the formation of each limb, the skeletal tissue musculature and nerves being derived from these segments. When, as in many fish, the radial muscles of the paired fins are formed from buds of the myotomes, their exact relation to the segments can be accurately made out. "Concentration," or the relative narrowing of the base of attachment of the fin, may introduce secondary modifications, which do not, however, affect the position of

the limb as a whole (12). The nerves supplying the radial muscles are branches of the spinal nerves corresponding to the myotomes from which the muscle-buds were developed; and the course of these nerves in the adult necessarily indicates the source of the fin muscles they supply, while their size is proportional to the amount of muscle derived from each particular segment. This is the case even when neighbouring muscular segments fuse to compound muscles, as usually happens in paired limbs.¹ The branches of the segmental spinal nerves may combine more or less completely to form a complex limb-plexus, but they nevertheless preserve their original connections with the spinal cord, and also their original peripheral connections with the muscle-substance derived from their own segments. It follows that the nerve-supply in the adult is a safe guide in deciding both which segments have been concerned in the formation of the limb, and in what proportion they have contributed to it.

We must conclude from these facts that the paired limbs do not bear a constant relation to any given segments in the Vertebrates, that they appear to shift along the segmented trunk, that this apparent shifting has taken place independently and repeatedly in the different classes, and that it can take place either forwards or backwards. For in the modern Anura the pelvic limb is almost undoubtedly farther forwards than in the ancestral Amphibian, and in the teleostean fish the more recent and modified forms may have the pelvic fin far forwards, until in extreme cases it reaches a position immediately behind the pectoral.

Not only do the paired limbs shift their position, but they also vary greatly in their extent, being sometimes formed by many and at other times by only a few segments. In the fishes this variation is extraordinary, and in Tetrapods it is less pronounced, but still considerable.

¹ In my paper on Fins (12) I maintained, against the views of Braus and others, that the radial muscles preserved the original segmentation. But this is not the case, and the error was corrected in a subsequent paper (15).

Or to put the matter in a more general way—suppose we call the consecutive segments A B C D . . . In one case the limb may belong to segments A B, in another to segments B C, and in a third to segments C D, and so on. Again in one animal a limb may belong to segments E F, in another to segments C D E F G, and in a third to segments A B C D E F G H. How are we to reconcile these facts with our conception of homology?

Some anatomists seem to consider the paired limbs and limb-girdles as special organs developed outside the truly segmented region of the body, as it were independent of it, and therefore capable of moving from one region to another. But this view is quite inadmissible; as already pointed out above, it is directly contradicted by the well-established facts of anatomy and embryology. The limbs are as truly segmented as the myotomes and vertebral column, and are formed from the same materials. The segmentation may, of course, be obscured in the adult, just as it may be in the trunk or head, but it is obvious in development. Moreover, the limbs never really abandon the segments from which they originated (12). It certainly is not by a theory of the migration of ready-formed limb-material in the embryo that we can explain the shifting of limbs, or preserve our ideal of homology.

Migration during ontogeny may indeed occur, but to a very limited extent. The direction and amount of the migration is faithfully recorded in the adult by the course of the nerves supplying the limb. For instance in the frog the straining backwards of the pelvic plexus shows that the base of the hind limb was moved back with the elongation of the pelvic girdle. In such fish as the whiting, where the pelvic fins have attained a jugular position actually in front of the pectorals, their real place of origin is betrayed by the nerves which pass backwards to the spinal cord, crossing those supplying the pectoral fins (see Diagram 4).

Certain variations in the attachment of the pelvic girdle to the sacral vertebræ may be explained in the same way. In the salamander, as shown by von Jhering (17), the pelvic

limb is normally supplied by the sixteenth, seventeenth and eighteenth spinal nerves, and the girdle is attached to the sixteenth vertebra. Occasionally, however, while the plexus remains in the same position the sacral vertebra is the seventeenth. Thus the limb and girdle, which presumably developed from the same segments in the two cases, become connected with the vertebral column one segment farther back, their real place of origin being shown by the nerves. It is only such slight secondary shifting that the theory of migration during ontogeny can explain.

There remain three other possible explanations of the varying position of limbs to be considered: the theory of intercalation and excalation, the theory of re-division, and the theory of progressive modification or transposition.

The theory of intercalation has been admirably dealt with by von Jhering in a classical memoir (17). According to this view, the relative shifting of a limb and its plexus along a series of segments in different animals is explained on the supposition that one or more segments have dropped out or new segments have been added between pre-existing segments. This process is taken to account not only for the apparent motion of a structure up or down the segmental series, its change of position, but also for the extension of a limb or plexus over more or fewer segments than it originally occupied. It is necessary to suppose that segments can be intercalated or excalated at any point in front of a plexus, within the plexus, or behind it.

Von Jhering first deals with such simple cases as *Sorex*, where a whole segment seems to have been intercalated in front, some individuals having thirteen and others fourteen dorsal vertebrae, the whole pelvic plexus and sacrum in the latter being situated one segment farther back. Or, again, *Cynocephalus*, in which the last lumbar vertebra and its nerve appear to have dropped out, leaving the plexus reduced by one nerve, and the pre-sacral vertebrae twenty-five instead of twenty-six in number. At first sight the theory seems to afford a plausible explanation of such variations. Less easy

is it to explain the next set of cases, in which the plexus is modified in extent or position without an accompanying change in the vertebral column. For instance, in the rabbit the lumbo-sacral nerve-plexus may in some individuals include numbers 25-30 and in others numbers 24-30, while the first sacral vertebra is the twenty-seventh in both cases. Here a nerve seems to have been intercalated in the middle of the plexus, since the crural nerve (coming chiefly from 26 and 27 in the first case) appears to have moved one segment forwards, the ischiadic remaining behind in its original position.

To account for these changes, von Jhering has to make another assumption: it is that the nervous system being derived from the epiblast and the skeleton and muscles from the mesoblast, they can vary independently, and that a segment having been intercalated or excalated in the series of nerves, a re-arrangement takes place so that the plexus fits again on to the unaltered vertebral column in a new position. The nerves slip a cog, so to speak, and catch on in a new place. The whole theory becomes very artificial. By the dropping out now of nervous segments, and now of skeletal segments, and again of complete segments comprising both elements, it seems possible to explain almost any conceivable variation in the disposition of these parts. But what evidence is there to support these assumptions? none whatever.

If the difficulties are great in the way of explaining the varying position of the limbs in these simple cases, they are formidable indeed when applied to those forms in which the differences are more pronounced, as, for instance, in the fishes. The smelt, *Osmerus eperlanus*, has a pectoral fin supplied by the spinal nerves 1-4, and a pelvic supplied by nerves 18-29 (Hammarsten, 16), while in the whiting, *Gadus merlangus*, the nerves 1-4, supply the pectoral fin, and nerves 5-6 the pelvic (Diagram 3). Again, in *Scymnus* the pectorals are supplied from nerves 2-18, and the pelvics from nerves 23-35; in *Torpedo* nerves 4-30 supply the pectoral, and nerves 31-42 the pelvics (Diagram 2). If the

approximation of the pelvic fin to the pectoral had been brought about by the excalation of segments, we should have to assume that the whole trunk region between the two had been suppressed in *Gadus* and *Torpedo*—an obviously absurd assumption, as Fürbringer has already pointed out. Moreover, twenty-seven new segments would have to be intercalated in the region of the pectoral fin of *Torpedo*. Now since such vast differences frequently occur between closely allied forms, we should have to suppose that this wholesale appearance or disappearance of segments takes place rapidly and repeatedly. If such were really the case, should we not expect to find some indication of the process—zones of growth or zones of reduction, where new segments would be forming, or old ones vanishing? No trace of such zones is found, either in the adult or in the embryo.¹ On the contrary, segments are found to grow only at the extreme end of

¹ It may, of course, be suggested that segments can be intercalated and exalated in the course of phylogeny just as they appear to be in ontogeny. But the two processes must be clearly distinguished. First of all there is, I believe, no evidence that segments are ever intercalated in ontogeny. Observation seems to have established that new segments are only formed at the growing end of the series. On the other hand, it is obvious that segments may be more or less completely crushed out in ontogeny—as, for instance, in the occipital region (see below). But it must be remembered, however, that these segments are, as a rule, clearly formed in early stages of development, and that our inability to make them out in later stages is mainly due to practical difficulties of observation and technique. The work is done on a series of individuals killed at various stages of development; often the series is incomplete and the stages separated by wide gaps. Could we observe one individual continuously, we should probably be able to trace out the fate of each segment with certainty. As a matter of fact the somites of the occipital region are generally distinct enough in the early stages of the most modified Craniates. Still, it may be supposed that if the process of reduction began earlier and earlier in successive generations, the crushing out might at last take place at the very beginning of growth, and that these segments might finally cease to appear at all as such. It would be rash to say that this has never happened; but, so far as I know, there is no convincing evidence that it has ever been the fate of segments in the Vertebrata.

the series.¹ It is difficult to see how some 300 segments could be intercalated in the trunk of a snake such as *python* without the formation of some zone of growth; yet no such zone is present. But it may be answered that the appearance in some specimens of incompletely double vertebrae shows how new segments could be added one by one. Such occasional abnormalities, however, do not necessarily indicate the mode of formation of new segments; they can be more easily explained as due to partial fusion and incomplete development, or as pathological phenomena induced by early injury.

We have seen to what absurd conclusions the theory of intercalation would lead us if applied to the vertebrates as an explanation of the variation in position of the paired limbs and girdles. The whole theory is based on too narrow and rigid a conception of homology. It assumes that a structure α is definitely and unalterably related to a given segment x , which can be traced from one animal to another; that wherever α is found there also must be x . When α changes its position it is then necessary to suppose, for the sake of preserving its strict homology, that x has moved with it. This results in the paradox that to preserve the homology of the limb, we are obliged to sacrifice the homology of whole regions—in some cases of nearly the whole trunk. And even then the strict homology of the limb (say the pectoral of *Torpedo*) is not really saved. The sacrifice has been all in vain, for new segments have been added to it (seventeen in the case of *Torpedo* as compared with *Scymnus*; see Diagram 2). It is really quite futile to attempt to define the homology of an organ in a segmented body by its ordinal position in the series of segments.²

¹ Segments appear to be always added at the posterior end; but they may be retarded in their development at the anterior end, as in the case of the head somites of the Craniate.

² From the point of view of a study of variation Bateson rightly maintains "the impossibility of applying a scheme of homology between individual segments" p. 128 (1).

Further, the theory cannot afford even a formal explanation of the change of position of the median fins relative to the paired fins in fishes, as I have already pointed out elsewhere (12). The median fins in Elasmobranchs are similar in structure and development to the paired fins, and, like these, shift up and down the body in different forms. Now the interesting and quite conclusive fact to notice is that the two sets of fins shift independently. For instance, the first dorsal fin is opposite the pectoral in *Lamna*, between the pectoral and the pelvic in *Alopecias*, opposite the pelvic in *Scyllium*, and behind the pelvic in *Raja*. If it is granted that the fins are homologous in these four genera, no addition or suppression of segments can possibly account for their disposition. Other cases of homologous organs passing in front or behind one another could be given.

The evidence against the theory of intercalation is overwhelming. Moreover, it undermines the very foundation of the definition of homology it is intended to uphold; for if segments can be added to or removed from any part of the series, there is no guarantee that any one particular segment in one individual really corresponds to any particular segment in another individual.

Let us now briefly examine a view which may be called the theory of re-division. It may be stated as follows: if one individual is composed of, say, twenty segments, and another of twenty-one, the difference is due, not to the addition of a new segment, but to the subdivision of the individual in the first case into twenty segments and in the second case into twenty-one segments. Therefore, no segment of the first individual can be strictly homologous with any segment of the second. If the number of segments is sufficiently increased by further subdivision into twenty-two, twenty-three, and so on, an organ originally situated on, say, the fifth segment might later on be found on the sixth or seventh; and two organs originally close together might become separated by a larger and larger number of segments. Although this theory may appear promising at first sight, it soon becomes obvious that it could only apply to the

very simplest cases, and is quite incapable of accounting for the relative shifting of organs accompanied by the unequal variation of segments in different regions. Whether we measure an object in inches or in centimetres the relative position of its parts remains unaltered. Only could there be relative shifting if the redivision was unequal along the series. Comparing, for instance, the vertebral column of *Dromaeus* with that of *Struthio*, we might say that in the former the cervical region has been divided into eighteen and the lumbar region into six segments, while in the ostrich the cervical region has been divided into seventeen and the lumbar into eight segments. Obviously this would be no explanation at all, but merely a statement in different words of the original problem we set out to solve. No doubt such a view avoids the difficulty of zones of growth or of reduction; but no more than the theory of intercalation can it be applied to such cases as the apparent suppression of the mid-region of the trunk in fishes where the pectoral meets the pelvic fin, or the independent shifting of the median and paired fins discussed above. Some theory of the redistribution of the formative substances to which morphological differentiation is due is necessary if we are to explain homology; mere redivision does not help us at all.¹

If neither migration nor intercalation nor redivision can account for the change in position of fins or paired limbs, there remains the theory of transposition (12 and 13). Fürbringer has shown how the nerve-plexus of a limb may become more or less extensive by the gradual assimilation of the nerves of neighbouring segments (9). Nerves at the anterior or posterior end may increase in size, and new nerves from adjoining segments may enter into the composition of a plexus; so that by gradual growth a limb originally supplied by, say, nerves E F G, may come to be supplied by nerves D E F G H, C D E F G H J, and so on. Or, on the contrary, by a similar

¹ It may well be doubted whether "redivision" ever takes place. When the total number of segments varies, the variation may better be interpreted as due to differences in growth—that is to say, to the addition or suppression of segments at the growing end of the series.

but reverse process of reduction, a limb originally supplied by nerves *c-j* may come to be supplied only by nerves *e-f-g*. If such were really the case we should expect to find the limits of a plexus somewhat indefinite and variable, the more important and stouter nerves towards the middle, and slenderer twigs contributed by nerves at each end. Now this is just what anatomical investigation reveals; a limb-plexus is built on this plan.

Further, a limb-plexus may shift, without altering its general structure, from one region to another, by such a process of growth or extension at one end accompanied by reduction at the other end. New segments being assimilated along the direction of growth, others may drop out, ceasing to contribute to the plexus. Thus a nerve-plexus may successively occupy segments *d-e-f*, *e-f-g*, *f-g-h*, and *g-h-j*. By a gradual process a plexus comes to occupy an entirely new position, having been transposed without the appearance or disappearance of any segments at all. What is true of the nerves is doubtless true also of the musculature and skeletal elements (Diagram 5). The fact that the position of a nerve-plexus and the size of its component nerves is an accurate guide to the segmental composition of a limb has already been sufficiently dwelt upon above.

This theory of the shifting of a plexus and a limb from one region to another is in complete harmony with the teaching of comparative anatomy and embryology. It is the only theory which gives a reasonable explanation of such cases as *Raja* and *Gadus*, and the independent motion of the paired and unpaired fins mentioned above. The process whereby the transposition¹ is brought about may be interpreted as due neither to the insertion or removal of segments nor to the

¹ To the correspondence between two similar sets of nerves forming a plexus, but occupying different ordinal positions in the series of segments, Fürbringer has applied the word Parhomology. This term, however, seems to imply that the homology is incomplete, whereas it is here contended that it may be as complete as between any two organs. Fürbringer also applies the term "imitative homodynamy" to the

migration of parts after the segmentation has been laid down in ontogeny, but to a redistribution at some very early stage in the unsegmented embryo of the formative substances.

It is quite clear, then, that the conception of homology in a segmented vertebrate is independent of any consideration of the number or ordinal position of the segments which compose the parts under comparison. If organs to be called homologous have to be composed of the same segments, we should have to conclude that the pectoral limbs of birds and reptiles are not homologous—which is absurd. It is merely an unnecessary complication to introduce the idea of segmental correspondence into a definition of homology. The heart, the liver or the lungs are held to be fully homologous throughout the Craniata, quite irrespective of any possible relation to segments; in the same way the pectoral limb of a reptile and of a bird may be called homologous merely as being corresponding parts of common origin. And so it is with other parts of the body; the various regions of the vertebral column, in so far as possessed by a common ancestor, are homologous, but they are not necessarily composed of the same segments.

Let us now consider the case of the occipital condyles, which seems to present greater difficulties. There is abundant evidence among the Pisces that the posterior limit of the head is variable, that more segments are assimilated into the head region in some fish than in others, that by growth and differentiation, by a process of transposition strictly comparable to that of fins, the hind limit of the head moves up or down the segmental series. More or fewer segments become included in the occipital region, more or fewer gill-slits develop and are supplied by a corresponding number of branches of the compound vagus nerve. Transposition can account for all these changes.

assimilation of one segment to another when it takes on the form and function of another. Bateson calls this homeosis (1), but it seems to me difficult to apply this term to the transposition of a structure which occupies one segment only.

But the interpretation of the occipital region is complicated by the well-established fact that one or more myotomes immediately behind the auditory capsule may undergo degeneration during ontogeny. These are the myotomes corresponding to the glosso-pharyngeal, the first, and the subsequent vagus dorsal roots, and supplied by the ventral spino-occipital roots. They tend to disappear in development from before backwards, and their nerves go with them. It might be thought that here at last we have a case of exalcation.¹ Indeed, Fürbringer himself, if I understand him rightly, seems to believe that the most posterior spino-occipital nerve, *z*, shifts forwards by the disappearance in phylogeny of the more anterior roots *s*, *t*, *u*, etc.

The process of ontogenetic degeneration of myotomes in the occipital region must not be confused with exalcation. The glosso-pharyngeal supplying the first branchial slit, and the first root of the vagus supplying the second slit, form a well-differentiated nerve complex which can be homologised throughout the craniate vertebrates. If the shifting of the hind limit of the head is to be attributed to the disappearance of segments behind the auditory capsule, then it is clear that (unless we sacrifice the homology of the glosso-pharyngeal and first vagus and their slits for the sake of saving that of the occipital segment) we must suppose that the segments have vanished, not at the anterior end of the metacotic series, but in the middle region—that is to say, between the first vagus root and the condyle. This supposition is directly against the evidence of embryology, which plainly shows that the more anterior segments are more degenerate than the posterior. We should also be compelled to assume that the change of position of the occipital condyle, being due to the disappearance of segments, could take place in one direction only—towards the anterior end. It would follow that the forms with an occipital region containing few segments have always been derived from those with many, which is in the highest degree improbable.

¹ See footnote, p. 241.

As in the case of the limbs, the theories of intercalation or redision fail utterly when applied to the occipital condyles. The segmental homology of the condyles cannot be saved by such means without sacrificing the homology of other structures of equal importance.

Turning now from these general considerations to the comparison of the condyles in the Amphibia and Amniota (15). There appear to be not more than three mesoblastic segments between the occipital condyle and the auditory capsule in the amphibian, and not less than five in the amniote.¹ If the condyle is on the same segment in the two groups, two segments must have disappeared in Amphibia. These cannot have vanished at the front end of the series, as already pointed out above, unless the glosso-pharyngeal and vagus nerves, etc., are new in the amphibian—not homologous with those of the amniote—a supposition which is obviously not admissible. There is absolutely no evidence in embryology that the segments have disappeared between the vagus and the condyle; but for the sake of argument let us suppose that they have. Does this help us out of our difficulties? Certainly not! On the contrary it lands us in a worse position than before. For it must then be supposed that the fourth branchial slit of the amphibian corresponds to a sixth of the amniote, and the whole homology of the branchial arches and other connected structures is upset. And we are further met with an insuperable difficulty concerning the hypoglossal

¹ The results of most authors who have studied the composition of the occipital region of the Amniota are remarkably uniform. Van Bemmelen (3), Corning (6) and Sewertzoff (19) in reptiles, Froriep (7), Belogolowy (2), in birds, find four myotomes in the embryo. The first is quite vestigial and belongs to the second meta-otic somite, since the first somite corresponding to the glosso-pharyngeal nerve is much reduced and never forms muscle (see Diagram 6). In mammals there appear to be also five somites and three distinct myotomes (Frorip (8) and others). A varying number of ventral nerve-roots join to form the hypoglossal. The first spinal (or post-occipital) still contributes to it in the reptiles and birds, but in the mammalia the hypoglossal roots are entirely intra-cranial.

nerve. This nerve, or complex of nerves, belongs with the various parts it supplies to a region extending in the Amphibia behind the occipital condyle to the second spinal nerve (the hypoglossal in the frog comes out between the first and second vertebræ—see Diagram 6)—and in front of the first vertebra in the Amniota.¹ The independent transposition of skeletal and neuro-muscular elements can alone account for such relative displacement.

Of course the whole question of the homology of the condyles in the Amphibia and Amniota may be avoided by supposing that they have been independently developed in the two groups, are not homologous, and have not altered their position since they made their first appearance. But, although we are not able to prove with absolute certainty that the common ancestor already possessed a skull with differentiated occipital region and well-defined condyles, yet the evidence points strongly to this conclusion. The reptiles and stegocephalous Amphibia merge into each other in the Permian and Carboniferous strata, and for my own part, I am firmly convinced that they are all derived from some common terrestrial ancestor with well-developed condyles. However, even supposing this was not the case, we should still be met by the difficulty of the hypoglossal. And since the common ancestor cannot be held to have been provided with several condyles, one of which remains in the amphibian and the other in the amniote, the theory of transposition seems to be the only one applicable in this case, as it has already been shown to be in the case of the fins.

The conclusion to which we are driven is that the occipital condyles of amphibians, reptiles, birds and mammals are all homologous, whatever may be the segments on which they are developed. They are fully homologous in the only sense in which homology can be practically defined, namely in the sense that they can be traced back to a common ancestor. In the course of evolution the function of condyle-formation, originally belonging to segment n of the series, has been transposed to segments $n+7$ or $n-7$. The transposition of the

nerves and other parts may or may not have accompanied that of the condyles.

Thus a consideration of the condyles, like that of the regions of the vertebral column or limbs, inevitably leads us to the conclusion that homology is independent of ordinal correspondence in segmental position. Specialised organs or any differentiated parts are truly homologous in different animals when they are derived from corresponding parts in the common ancestor—the animals being compared as wholes and not their separate segments. And this is true whether these organs or parts are composed of few or of many, of the same or of different segments, or are not segmented at all.

On the other hand, any attempt to define homology as complete only when including strict segmental correspondence defeats its own object. It is doubtful whether any organs or parts whatsoever could be proved to be completely homologous in this sense; certainly not the paired limbs, nor the regions of the vertebral column, nor the occipital condyles. Even when homologous organs appear to be composed of the same segments, the appearance may be deceptive; for if any form of multiplication or of intercalation of segments can take place, the comparison of segment with segment becomes at once uncertain.

To advocate the view that homology must be considered as independent of segmental correspondence is the object of this paper; but in conclusion a few words may be said concerning the possible connection between them. It is a remarkable fact that a constant relation often becomes established between certain segments and certain organs or differentiated parts.

The various cranial nerves, for instance, appear to bear a fixed relation to the anterior segments of the head throughout the Craniata. The muscles of the eye, the ear, the jaws, the gill-slits, etc., are all definitely related to certain segments, more or less closely and in different ways. The neck of mammals (with but three exceptions) is formed of seven segments, the last lumbar vertebra of the Artiodactyle Ungulates is always the twenty-sixth, the vertebral column of the

Teleostean family *Triacanthidae* is composed of twenty vertebrae, and so on. Undoubtedly a correspondence of this kind may become established, but it appears to be of secondary importance. Generally speaking it is more definite and invariable in the anterior than in the posterior region, and in regions or animals composed of few than in those composed of many segments. It is just as if Nature got tired of counting towards the tail end of a developing animal, and as if her arithmetic became uncertain when dealing with large numbers. But structure and segmentation vary independently, and whatever may be the connection which becomes established between them, and however close it may be, it would seem that we must not consider it as constant and essential.

In the segmented vertebrate the materials for the formation of muscular nervous and skeletal segments are distributed along the body; those particular segments which occur in appropriate positions are entrusted, so to speak, with the development of special organs. The function of producing an organ may be transposed from one segment to another. How this transposition is brought about we do not know as yet; possibly it is accompanied by the redistribution of organ-forming substances at a very early stage, regulated by a complex of stimuli subordinated to the needs of the individual as a whole.¹

¹ What has been said of the Vertebrates would probably apply equally well to the Annelids or Arthropods. Although their segmentation may very well have been quite independently developed, yet it resembles that of the vertebrate in that segments appear to be always increased or diminished in number at the posterior end of the series. The same specialisation of segments, of appendages, and of other repeated parts takes place, and the same apparent shifting. In these also it is to be explained by transposition. Any appropriate segment in the series may be called upon to develop a particular kind of appendage or a genital duct, for instance, and the number of these organs may be increased or diminished without a corresponding change in the whole number of segments. We may speak of a general homology of the several series of repeated parts, and of a more special homology of any one of them which, like the mandible or green gland or oviduct, may be traced to a common ancestor. Just as in the vertebrate, so in the annelid and arthropod, a very constant relation may be established.

But then, it will be objected, is homology to be reduced to a vague and almost meaningless comparison? Not at all! Comparing a horse with a man, we may say that the trunk of the one is generally homologous with the trunk of the other; further, that the fore limb of the horse is homologous with the fore limb of man; and further still, that the one digit of the former is more specially homologous with the middle digit of the latter, and so on to the minutest detail—to the smallest blood-vessel, to a single nerve-fibre, even to a single cell. The homology may be perfectly definite, and pursued to the furthest conceivable limit. For it to be recognised it is only necessary that the structures compared should, at all events in theory, be traced to a common ancestral origin.

The completeness of the homology depends on how far all the parts can be so traced back. The homology is impaired by the addition or loss of any parts. For instance, the pectoral girdle of the Teleostome fish is incompletely homologous with that of the Elasmobranch, since dermal bones of different origin have been added in the Teleostome to the primitive endoskeletal girdle, and it is incompletely homologous with the pectoral girdle of the mammal, because the latter has almost or entirely lost the dermal elements. Two organs are completely homologous when all their parts have been derived from corresponding parts in the common ancestor.

SUMMARY.

In the Vertebrates, as in other animals, the organs and parts of two individuals are to be considered as homologous when they can be traced back to corresponding parts in a common ancestor, and not because they occur on the same segments.

between these organs and segments of a certain numerical order; and this relation is also more often found in animals composed of few segments than of many, and at the anterior than at the posterior end of the body (see further the articles on Arthropoda and Metamerism written by Sir E. R. Lankester in the 'Encycl. Brit.', eleventh edition, and reprinted in this journal, vol. 47).

The homology is independent of the number and ordinal position of the segments which take a share in the formation of the organs. Any structure may apparently shift from one segment to another; and this is brought about neither by intercalation or excalation of segments, nor by redivision, nor by migration, but by a process of transposition. Organs may be homologous when they are composed of few or of many, of the same or of different segments, or are not segmented at all. There are degrees of homology: it may be general or more special, complete or incomplete. The homology of two organs is complete when all their parts have been derived from corresponding parts in a common ancestor.

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EXPLANATION OF PLATES 15 AND 16,

Illustrating Mr. Edwin S. Goodrich’s paper, ‘Metameric Segmentation and Homology.’

PLATES 15 AND 16.

Diagram 1.—The position of the paired limbs as shown by the nerve-supply. The line *o* represents the hind limit of the head. The spinal nerves contributing to the limb plexus are numbered. The range of the pectoral plexus is covered by a continuous line, that of the pelvic plexus by a broken line. *S* shows the position of the sacral vertebrae.

Diagram 2.—The position and extent of the paired fins of *Torpedo* and *Scymnus* as shown by the nerve-supply (from the observations of Braus). A continuous line covers the pectoral plexus and a broken line the pelvic plexus.

Diagram 3.—The position and extent of the paired fins of *Osmerus eperlanus* (after Hammarsten) and of *Gadus merlangus*. The first nerve in the former and the first two nerves in the latter pass through the skull.

Diagram 4.—The nerve-supply of the paired fins of *Gadus merlangus*: *A* in their natural position, and *B* with the pelvic brought back to its place of origin.

Diagram 5.—Three figures illustrating the principle of transposition as seen in the development of median fins. From the myotomes *m* are derived the radial fin-muscles *r.m.* 1-11 branches of spinal nerves.

Diagram 6.—The head-region of an Amphibian *A*, and an Amniote (mammal) *B*. The broken line *o-o* indicates the hind limit of the occipital region. 1-7 myotomes. *a*. Auditory capsule. *br.s.* Bronchial slit. *f.* Facial nerve. *gl.* Glosso-pharyngeal. *h.* Hypoglossal. *h.m.* Hypoglossal musculature. *n.a.* Neural arch. *n.c.* Nasal capsule. *o.p.* Optic capsule. *s.* Tympanum. *s.g.* Vestigial spinal ganglion. *s.o.* First metaotic somite. *sp.* Spinal nerve. *tr¹.* Profundus. *tr²* Trigeminal. *v.* vagus nerve.

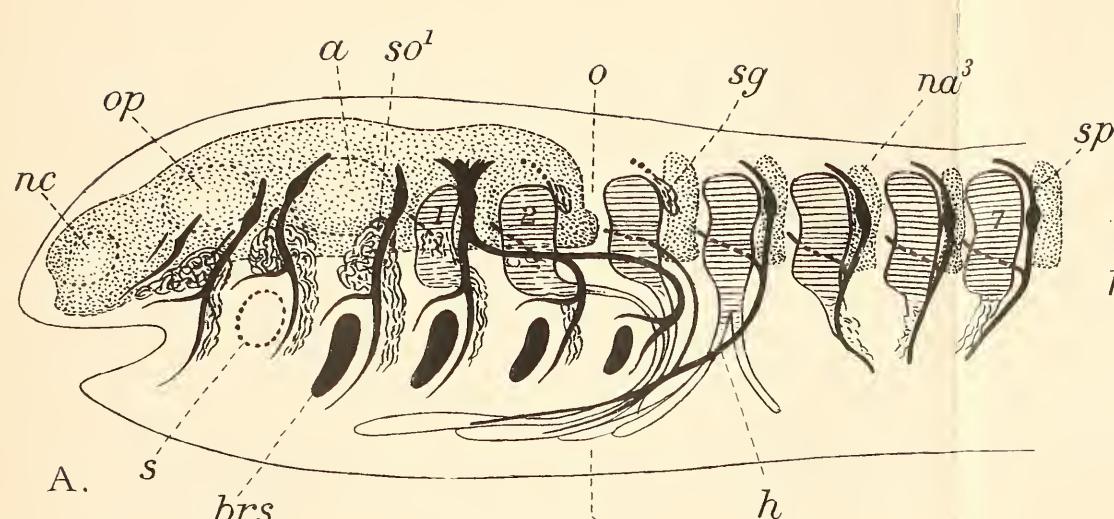


DIAGRAM 6.

GOODRICH — METAMERIC SEGMENTATION.

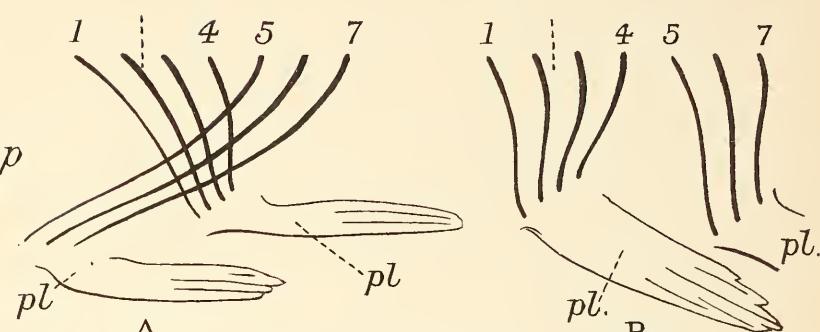


DIAGRAM 4.

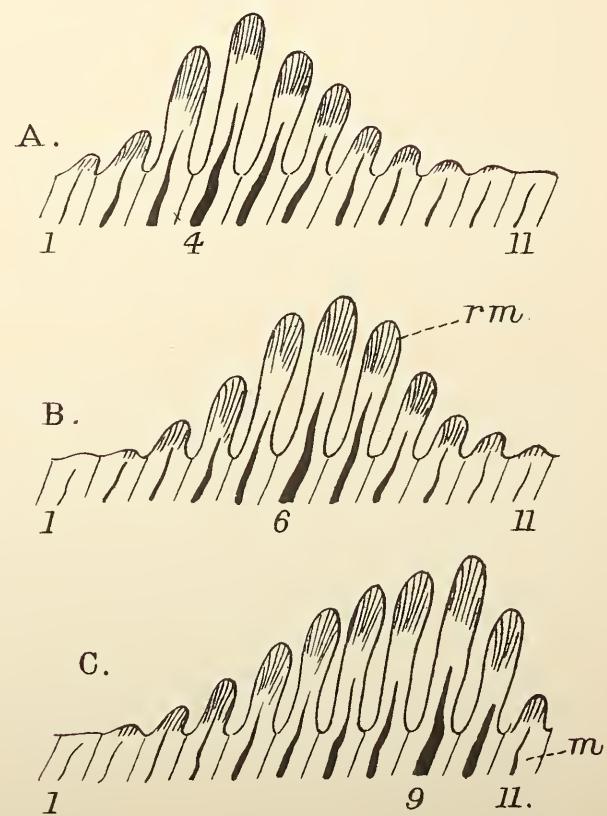


DIAGRAM 5.

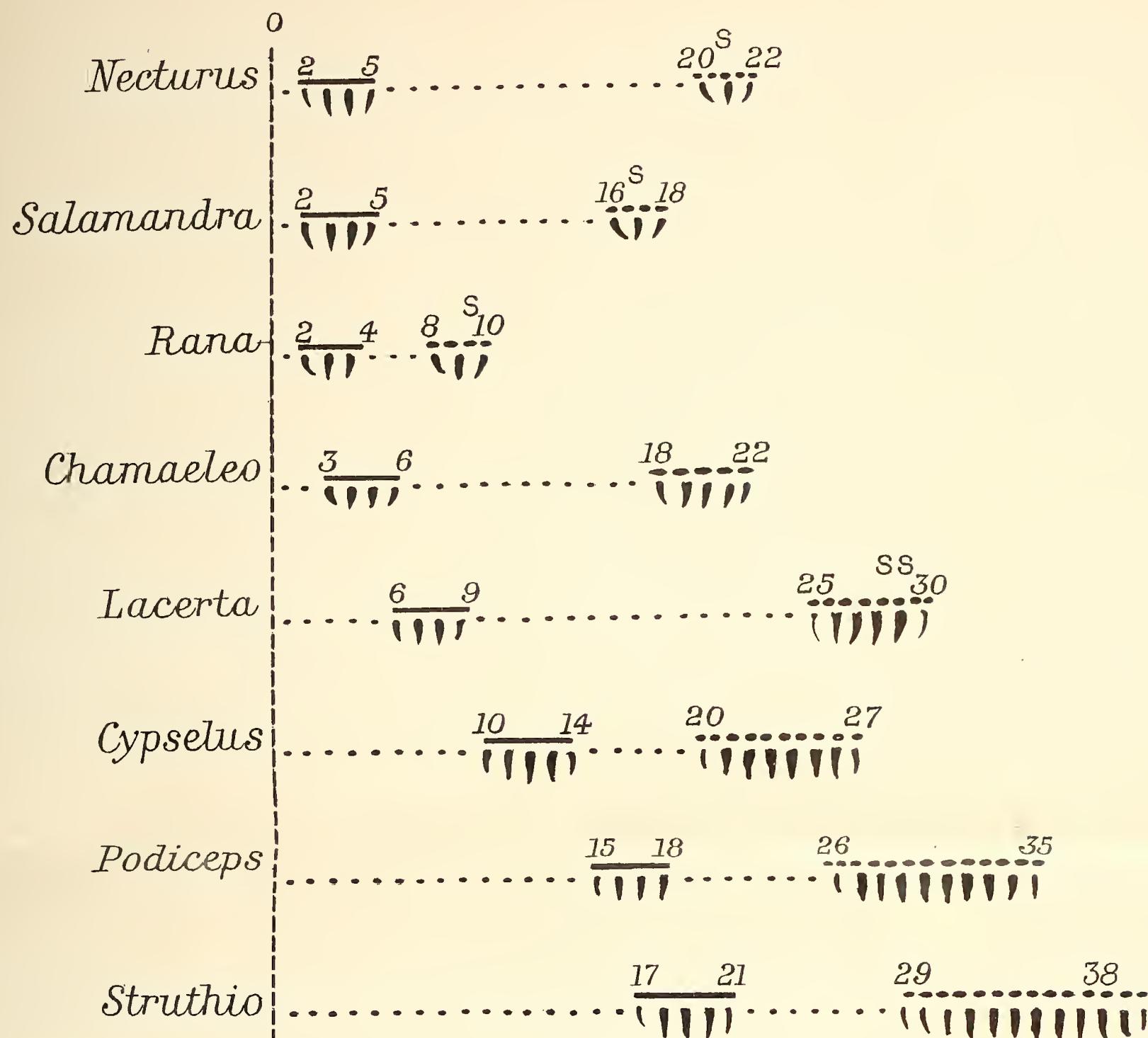


DIAGRAM 1.

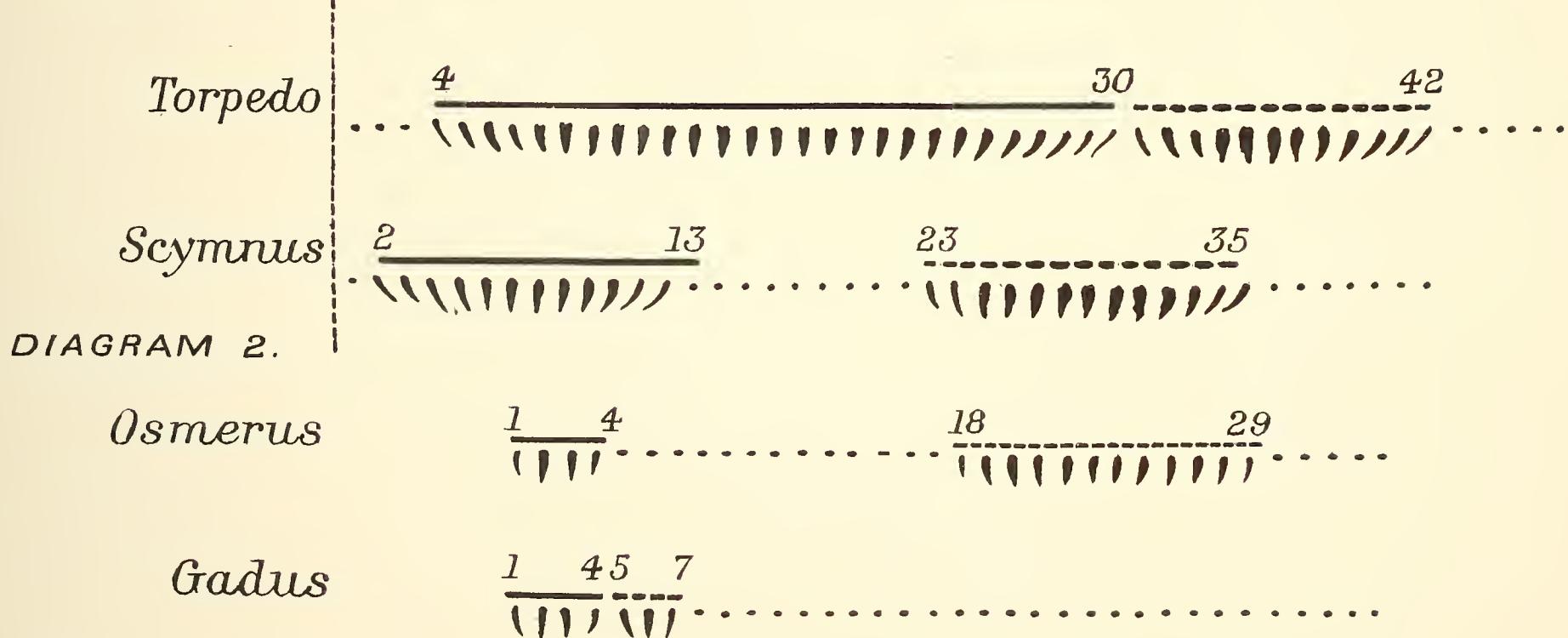


DIAGRAM 3.